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TOAD AND FROG ROD PHOTOCURRENTS

J.D. CONNER*

Ophthalmology Department, University of Michigan Medical School, Ann Arbor, MI (U.S.A.)

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The size of *Bufo marinus* and *Rana pipiens* rod photocurrents is similarly affected by changes in flash intensity. These species' rods also produce similar photocurrents during steady illumination, to which they both adapt. Thus, their transduction mechanisms are probably alike. Previous reports that frog and toad rod responses are different may have resulted from the use of an unusual procedure in which the rod outer segment was isolated from its inner segment.

Recent suction electrode measurements of toad rod photocurrents by Baylor et al. [1] and of frog rod photovoltages by Jagger [5, 6] agree that the amplitude, R, of a photoresponse is related to the intensity, i, of the flash which caused it by

$$\frac{R}{R_{max}} = \frac{i^n}{i^n + i_o} \quad (1)$$

where R_{max} is the cell's largest photoresponse, and i_o and n are constants. These studies disagree regarding the value of the exponent, n, however, which equals one when Eqn. 1 describes toad responses and which equals two when it fits frog data. This discrepancy has led Jagger [5] to propose that models of frog rod transduction may need to substitute a second-order process for a first-order mechanism which presumably operates in the rods of many other vertebrates [1–3, 7, 8]. A fundamental difference between the rod transduction mechanisms of such closely related species would be important, and so a study of this difference was undertaken during which successive measurements of toad and frog rod photocurrents were made.

*Present address: Department of Physiology and Biophysics, University of Washington Medical School, Seattle, WA 98195, U.S.A.

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Toad and frog eyes were enucleated and hemisected, and the eye cups were placed in a Ringer containing (in mM); NaCl, 111; $MgCl_2$, 1.6; KCl, 2.5; $CaCl_2$, 1.0; D-glucose, 10; HEPES, 3, buffered to pH 7.8 with NaOH. Retinas were removed from the eyecups and chopped into 1 mm chunks, which were transferred in Ringer to the stage of an inverted, compound microscope. There, under visual control, single rod outer segments were sucked into the barrel of a pipette, and membrane currents were recorded as described by Baylor et al. [1]. Flashes were produced by calibrated light-emitting diodes. Recordings were often stable for 2 h or more, and during them toad and frog rods showed comparable sensitivity and durability.

Ideally, rod responses of *Rana esculenta*, studied by Jagger [5, 6], and of *Bufo marinus*, studied by Baylor et al. [1], would have been compared. Unfortunately, *Rana esculenta* were unavailable, and *Rana pipiens*, a closely related species, were used instead. The amplitudes of the responses of 24 toad and frog rods have been plotted as functions of intensity in Fig. 1. The solid line in Fig. 1, which fits frog and toad data equally well, is the solution of Eqn. 1 when n equals one. The broken line,

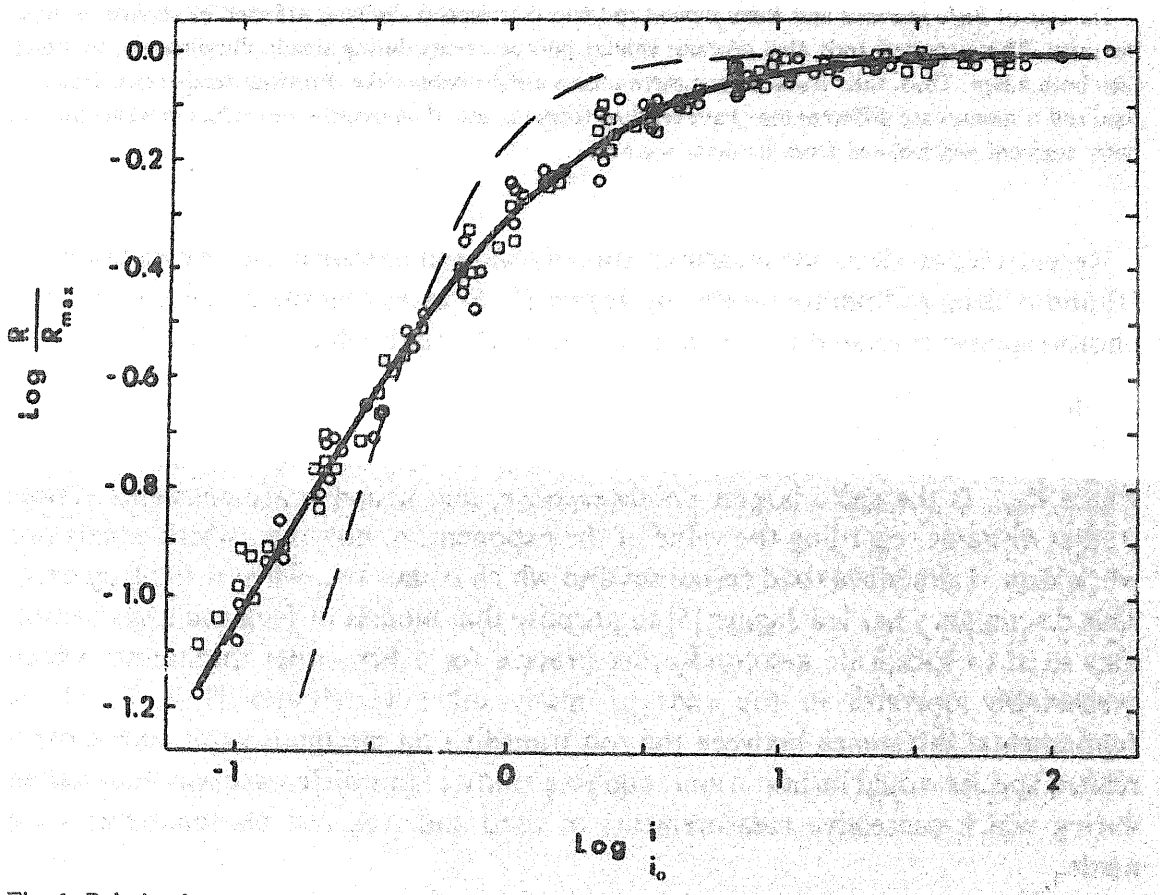

Fig. 1. Relation between normalized peak amplitude of the responses of 12 toad rods (squares) and of 12 frog rods (circles) and the normalized flash intensities which caused them. For toad rods R_{max} averaged 21.5 pA (S.E. = 1.15) and i_o averaged 8.9 incident photons/μm^2. For frog rods, R_{max} averaged 21.2 pA (S.E. = 1.01) and i_o averaged 10.7 incident quanta/μm^2. Stimuli were 100 msec flashes of nonpolarized 560 nm light.

which fits neither frog nor toad data, is the solution of Eqn. 1 when n equals two. Thus, the relation of response amplitude to flash intensity for *Bufo marinus* and *Rana pipiens* rods is identical, and it is likely that their underlying transduction mechanisms are alike. In this way *Rana pipiens* rods apparently differ from those of *Rana esculenta* as reported by Jagger [5, 6].

Rana pipiens and *Bufo marinus* rods share many other response properties, which supports the view that their underlying mechanisms are similar. First, both species' rods adapt so that flash responses are smaller and faster in light than in darkness and so that the step response often sags from an initial peak to a subsequent plateau. Second, noise in these species' rod photocurrents is suppressed by light. Third, when a bright light is extinguished, its desensitizing after-effects last longer in both *Bufo marinus* and *Rana pipiens* rods than the photocurrent it produced. Thus, the general similarity of the photoresponses of *Rana pipiens* and *Bufo marinus* rods suggests that their fundamental mechanisms differ only in quantitative detail.

The rod responses of *Rana pipiens*, reported here, differ from those of *Rana esculenta* which Jagger has reported [5, 6]. Perhaps these closely related species' rods may differ fundamentally in the way Jagger suggested for frog and toad rods, but it seems more likely that these different results are due to differences in the procedures used to obtain them. Here, responses were measured from the outer segments of intact rods, which were embedded in chunks of living retina. In Jagger's experiments, though, responses were recorded from outer segments which had been torn from their inner segments. Although these ruptured outer segments apparently resealed, their photocurrents may have been altered. For example, the Na^+–K^+ pumps of the rod membrane may contribute an electronic component to the outer segment's photocurrent [9, 10]. Since these pumps are concentrated in the rod's inner segment [4, 9, 10], an isolated outer segment's photocurrent would not contain this electrogenic component, if one exists. Thus, the photocurrents of isolated outer segments may differ from the photocurrents of intact outer segment. This, or some similar effect, may explain the difference between the results obtained here for *Rana pipiens* and those reported previously for *Rana esculenta* [5, 6]. Repeated efforts to study this interesting change by duplicating Jagger's method [5, 6] were unsuccessful. Although photocurrent were recorded from a few isolated rod outer segments, these were small and unstable, and they disappeared about 5 min. after the outer segment was separated from its inner segment. Thus, amplitude measurements based on them were unreliable.

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